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EVOLUTIONARY TENDENCIES AMONG GYMNOSPERMS

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The investigation of gymnosperms has proceeded with such vigor that some adequate picture of the group freed from its details may now be obtained. The confusion of details often obscures the important facts, and it may be of service, at this stage of our knowledge, to emphasize them. There is no better way in which to develop a clear picture of a great group than to select those facts of structure that enter into its general evolutionary history. This has nothing to do with differences among species, or even among genera, which may be left to the taxonomist; but it deals with those general tendencies to change structures which can be noted in passing from the most ancient gymnosperms to the most recent.

While the discovery of these tendencies aids in reaching conclusions in reference to the phylogenetic connections of the groups of gymnosperms, it must be remembered that the tendencies are facts and the phylogenetic conclusions are very uncertain inferences. Moreover, a general tendency expresses itself throughout a great group, and has to do with the transition from ancient to modern forms, rather than with the breaking-up of the group into several phylogenetic lines. Failure to remember this fact has been responsible for much sterile inference as to relationships, similar stages in some general tendency being assumed to mean immediate genetic connection. The organism is a plexus of structures, and must be considered in its totality when relationships are being considered. Among the general tendencies leading to the origin of seed plants, for example, that which resulted in heterospory must be regarded as of paramount importance;

and yet it is clear that heterospory arose several times, and probably many times, independently as the natural result of a general tendency among pteridophytes. To put into the same genetic group all heterosporous pteridophytes would be regarded now as a morphological absurdity; and yet there have been repeated suggestions of relationship, especially among conifers, on the basis of certain features of the female gametophyte, for example, features which represent a stage in a general change that may occur in a number of independent lines.

In passing from the ancient to the modern gymnosperms, it becomes evident that groups differ as to the rapidity with which they respond to a general tendency to change, and it, is this difference that helps to constitute groups. A modern group, for example, may associate a number of ancient features with others that are recent; or all of the ancient features may have been changed. This has been called the "lagging behind" of certain structures, but it should not imply that they are held back and will come forward later; it simply means that for some reason they have not responded to the general tendency among gymnosperms to change in a certain direction. The retention of an old structure must not be confused with the reappearance of an old structure. For example, it seems clear that the most ancient gymnosperms were large-leaved forms, from which the small-leaved conifers were derived; and yet small-leaved pteridophytes were probably more ancient than large-leaved ones. If this be true, the appearance of small leaves among conifers is the reappearance of an ancient feature, and not its retention. To prove the retention of an ancient feature demands the establishment of its phylogenetic continuity.

PHYLOGENY

Before sketching the general evolutionary tendencies among gymnosperms, it will be of service to outline what seems to be a reasonable conclusion as to the phylogenetic connections of the groups. This statement and those that follow will be all the more clear if freed from the details upon which they are based, and also from citations. Those who know the facts and the investigators do not need their recital; and those who do not know them would only be confused by their recital.

The Paleozoic groups Cycadofilicales[1] and Cordaitales represent the historical background of gymnosperms. They are of equal age, so far as the records are available, and are so connected by intergrading (or rather anastomosing) forms that their relationship seems evident. The Cycadofilicales are so fern-like in every feature except their seeds, that their derivation from some ancient fern stock (called provisionally Primofilices) is as certain as phylogenetic connections can be. The origin of the Cordaitales, therefore, presents two alternatives: either they arose independently from the same ancient fern stock, or they were differentiated from the Cycadofilicales very early. To choose between these alternatives is not very important, but the latter one seems to be the more reasonable, because the Cordaitales (as we know them) are much more removed from the ferns than are the Cycadofilicales. If this conclusion is accepted, it follows that gymnosperms began with Cycadofilicales more ancient than any yet known; that Cordaitales branched off from Cycadofilicales earlier than our present records; and that the two groups constituted the extensive gymnosperm flora of the Carboniferous.

This Paleozoic display of gymnosperms was succeeded by a Mesozoic display, in which at least four groups are recognized. From the Cycadofilicales there arose the Mesozoic Bennettitales and the Cycadales; and from the Cordaitales the Mesozoic Ginkgoales and Coniferales were derived. The Bennettitales have been traced almost to the Paleozoic, and their structure, as well as the habit of some of the earlier forms, make their connection with the Cycadofilicales appear convincing. The relation of the Bennettitales to the Cycadales is not so clear; either the two groups were differentiated from a common stock that arose from the Cycadofilicales and continued into the Mesozoic, or the Cycadales were differentiated early from the Bennettitales. The records show that the Cycadales are much younger than the Bennettitales, and were much more scantily represented during the Mesozoic; and therefore the latter alternative seems to be the more reasonable. In any event, the only question at issue is whether the gymnosperm stock which came from the Cycadofilicales into the Mesozoic is to be called Bennettitales or a Bennettitales-Cycadales plexus (a "common stock"); and it is altogether probable that this stock has already been assigned to the Bennettitales in the description of cycadophyte forms from the Triassic and Jurassic. In the gymnosperm flora of today, therefore, the Cycadales, although relatively a modern group, are the nearest representatives of the Paleozoic Cycadofilicales.

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[1] It seems impossible at present to recognize a group Pteridosperms as distinct from Cycadofilices, and there is a growing impression that the two groups are coextensive. Under the circumstances, it would seem proper to retain for the group the older name. It seems clear, also, that it should take its place as a group of gymnosperms coordinate with Cordaitales, Cycadales, Coniferales, etc.; for it is impossible as yet to construct a definition which would exclude it from gymnosperms on the basis of characters of so high an order as those which separate gymnosperms from angiosperms. For this reason, I have appended to the older name the termination that makes it conform to the names of groups of similar rank, and shall refer to it in this paper as the CYCADOFILICALES.

The Ginkgoales and Coniferales have both been traced into late and independent Paleozoic connection with the Cordaitales, and were well displayed during the Mesozoic. The Ginkgoales, while widely distributed during the Mesozoic, apparently were never a large group; and this group has continued as a single line into the present flora, and has retained certain features of the Cordaitales which the Coniferales have lost. The Coniferales, on the other hand, began that extensive differentiation during the Mesozoic which has resulted in six recognized tribes in our present flora. Among these tribes the earliest to be recognized are the Abietineae and the Araucarineae, and their very early separation is so evident as to raise the question whether they may not be independent in origin. In any event, the other tribes recognized in our present flora were of later origin; the Taxodineae and the Cupressineae, and possibly the Taxineae, arising from the Mesozoic Abietineae; and the Podocarpineae possibly arising from the Mesozoic Araucarineae.

The connections of the Gnetales are altogether obscure, and every opinion as to their origin must be regarded as very tentative. Although they have not been discovered as fossils, the great amount of differentiation they show and their widely scattered geographical distribution indicate a considerable history. Evidence seems to be accumulating that they may have been derived from the Cupressineae, or at least that they are closely related to that tribe in origin.

VASCULAR ANATOMY

The central cylinder of the Cycadofilicales, like that of ferns, was protostelic, siphonostelic, or polystelic. Whatever may be the genetic connection of these types of cylinder, the siphonostele is the type that was carried forward in the evolution of gymnosperms. This siphonostele was made up of collateral mesarch bundles, developed secondary wood composed of tracheids, and the bundles of all its peripheral connections were concentric or at least mesarch.

Among the gymnosperms the universal tendency was to eliminate the centripetal xylem, a tendency carried forward from the ferns, until the collateral mesarch bundles of the central cylinder became collateral endarch; and more gradually the bundles of the peripheral regions became collateral mesarch and finally collateral endarch. So early was this accomplished for the central cylinder that a collateral endarch cylinder is a feature of gymnosperms in general. From what has been said as to the variable rate of change among the members of a great group, it would be expected that mesarch and even concentric bundles might be found in peripheral parts of certain species of genera whose allies had completely eliminated centripetal xylem, or might occur occasionally in any species or genus. It is an interesting fact that centripetal xylem appears to linger longest in the cotyledons; and the number of gymnosperms in which it is known to occur in this organ, regularly or occasionally, is increasing rapidly.

In the development of secondary wood, the general tendency among gymnosperms is to increase it in amount, so that a thick vascular cylinder is built up by the primary cambium. This tendency is apparent among the Cordaitales, but it reaches its most conspicuous result in the Coniferales and Ginkgoales. This changed also the general topography of the stem, both pith and cortex being much reduced in relative amount. The Bennettitales and Cycadales responded feebly if at all to this tendency, one of their features being the retention of the general stem structure of the Cycadofilicales. In these groups the primary cambium is either short-lived or functions very slowly, and in some forms secondary cambium produces cortical bundles; but the formation of secondary wood never prevents the formation of a large pith and an extensive cortex. It is in these groups also that the concentric and mesarch bundles are most common in the peripheral members, being found somewhere in all forms; while among the Coniferales the centripetal xylem has been almost completely eliminated. In vascular anatomy therefore, the Cycadales have retained more ancient features than any other living group.

The vascular condition among Gnetales can hardly be spoken of in connection with general tendencies; but the appearance of true vessels associated with the tracheids of the secondary wood is too important to omit. In any event, these true vessels of the secondary wood suggest that in the evolution of the vascular cylinder the original tracheids of secondary wood are finally and gradually replaced by true vessels.

THE LEAF

The leaves of gymnosperms may be used to illustrate a structure that exhibits no general evolutionary tendency, but responds more or less directly to the conditions of living. The most ancient gymnosperms possessed ample, fern-like leaves, and under appropriate conditions this type of leaf persisted, as in the tropical cycads of today. The conifers, however, have developed a very different type of leaf, one that was well under way among the Cordaitales, and which reaches an extreme expression in small and rigid needles or concrescent scales. This cannot be regarded as the result of a general tendency among gymnosperms, quite unrelated to conditions of living, such as is shown by the persistent progressive changes of other structures. The leaf is too variable a structure, and too closely related in its work to external conditions to permit such an explanation of its changes.

It would be interesting to know the conditions in which needles and concrescent disks were established; but in the absence of any such knowledge, the sharply contrasted geographical distribution of Cycadales and Coniferales may suggest that the conditions of change were associated with the evolution of the land areas and of the climate of the temperate regions.

THE STROBILUS

The Cycadofilicales are the only gymnosperms without strobili. Although the sporophylls differ more or less from the fern-like foliage leaves or their branches, they are not aggregated into a strobilus distinct from the rest of the shoot. The organization of a strobilus by the shortening of the sporophyll-bearing shoot is a conspicuous feature of gymnosperms, and it must have been derived from the condition observed among the Cycadofilicales.

The Cordaitales were the first gymnosperms to produce strobili, and this is one of their conspicuous contrasts with Cycadofilicales. The record of the structure of their strobili is meager, but it shows several tendencies in strobilus-formation. Of primary importance is the fact that the strobili are monosporangiate, and this monosporangiate character prevails throughout the Ginkgoales and Coniferales. Among the Gnetales, a group probably related to the general coniferophyte phylum, amphisporangiate strobili occur in Tumboa. If this connection be accepted, therefore, these amphisporangiate strobili have been derived from monosporangiate strobili. It is not necessary to associate in one genetic connection all of the amphisporangiate gymnosperms, for that condition doubtless appeared independently several times, just as the monosporangiate strobilus is known to have appeared at least twice in distinct phyla (Cordaitales and Cycadophytes).

Another fact in reference to the strobili of Cordaitales, which must stand for the most ancient gymnosperm strobili, is that they included both simple and compound strobili. The staminate strobilus was simple, that is, its sporophylls were borne directly upon the axis of the strobilus; and this type of staminate strobilus persisted throughout the Ginkgoales and Coniferales. Among the Gnetales the staminate strobilus is compound, the individual simple strobilus being borne on axes of the second order in the axils of sterile bracts which make up the general strobilus. There is an evident relationship between the compact compound staminate strobilus, such as occurs in Ephedra and in Tumboa, and the short foliage branch bearing axillary simple staminate strobili, as in Torreya. Even in Gnetum the compound staminate strobilus is a loose one; and among the taxads there is a tendency to compact the staminate strobiliferous branch. The conclusion is that the staminate strobilus among coniferophytes is quite persistently simple, but that in the more modern members of the phylum it tends to become compound, a condition accomplished by compacting a short strobiliferous shoot.

The ovulate strobilus of Cordaitales was compound, at least in the very few specimens sectioned; that is, the ovules were borne on short secondary and bractlet-bearing axes that arose in the axils of the sterile and overlapping bracts that constituted the strobilus. This compound ovulate strobilus is a distinctive feature of the coniferophytes, prevailing among the Pinaceae and characterizing the Gnetales. That simple ovulate strobili may have been derived from it is quite possible. For example, in Torreya the ovulate strobili are simple and are axillary on short leafy branches, just such a branch as could have arisen through the elongation of the axis of a compound ovulate strobilus, so that the sterile bracts could be replaced by foliage leaves. It may be said that the change may have taken place in the other direction, and that the short leafy strobiliferous branch was compacted into a compound ovulate strobilus; but it must be remembered that the Cordaitales with their compound ovulate strobili are very old, and that the Taxineae with their leafy strobiliferous branches are relatively very recent. Of course it may be discovered that the Cordaitales included also forms with simple strobili on leafy shoots. This possibility is further emphasized by the fact that the ovulate strobili of the Araucarineae, and of their allies the Podocarpineae, are simple. The former tribe is a very old one, and its connection with the Cordaitales is either direct or nearly so, so that it is altogether probable that such ovulate strobili occurred in that group. The connection of the Taxineae with the Cordaitales, however, appears to be so remote, and their relation to groups with compound ovulate strobili seems to be so much more immediate, that it is more reasonable to suppose that their ovulate strobiliferous branches have arisen from compound strobili in the way described above.

Long after the Cordaitales had established their simple staminate and compound ovulate strobili, strobili appeared in the cycadophyte phylum, being found in Bennettitales and Cycadales; and even in the living Cycas the loose ovulate strobilus retains the evidence of its origin from the separated sporophylls of Cycadofilicales. The cycadophyte strobilus has always been simple, and this may be related to the more compact habit of body, with its lack of free-branching. The most remarkable feature of the early strobili of this phylum, however, is their amphisporangiate character, the two sets of sporophylls holding the same relation to one another that is held by the stamens and carpels of angiosperms; and this marks the Bennettitales as a unique group among gymnosperms. The monosporangiate tendency, however, which characterizes the coniferophytes, is shown by the Cycadales among cycadophytes, and it was either established directly, or it arose from an early differentiation of the amphisporangiate strobilus of the Bennettitales. The evidence of history favors the latter view, but the probabilities of the situation favor the former. In any event, both monosporangiate and amphisporangiate strobili were established among cycadophytes.

THE STAMEN

Among gymnosperms the stamen may be regarded as a very conservative structure, retaining throughout most of the phyla its fern-like characteristics. Its form perhaps became almost as much differentiated among the Cycadofilicales as it ever became among gymnosperms. In this primitive group, in addition to microsporophylls resembling fern-like leaves with abaxial synangia, there appeared others that have been spoken of as the Crossotheca ("epaulet") and the Calymmatotheca ("cupule") types, and in all probability still others will be discovered. All of these types were continued among the coniferophytes, with varying details of minor importance. Among some of the Gnetales, either the sporophyll has become very much reduced, or it has become suppressed, so that the microsporangia are cauline; but even in Tumboa the old terminal synangium is evident.

Among the cycadophytes, on the other hand, only what may be regarded as the most ancient type of microsporophyll has been retained, that is, the fern-type with abaxial sporangia (often synangia). Among the Bennettitales, there is so little departure from the old type that their microsporophylls resemble pinnate fern leaves with abaxial synangia; and even among the Cycadales the more or less leaf-like microsporophylls show the same character. If there is any tendency in the stamens of this phylum worth noting, it is the tendency shown among the cycads to reduce the sterile apex of the sporophyll to a more compact peltate expansion.

The microsporangium of gymnosperms is a very consistent structure, originating from the hypodermal layer of cells, and developing a wall of several layers, the innermost one of which is usually differentiated as the tapetum. The only general tendencies to be observed are the gradual replacement of synangia by separate sporangia, and the more rapid elimination of all evidences of an annulus (in the general sense). It is noteworthy that in both these particulars the cycadophytes, with their much more recent connection with the Cycadofilicales, are far behind the coniferophytes.

THE OVULE

The origin of the ovule of gymnosperms remains in obscurity. While the stamen and its sporangia repeat the corresponding structures of ferns, the ovules of Cycadofilicales and of Cordaitales are so well organized, even in the modern sense, that their connection with the sporangia or synangia of ferns is entirely a matter of inference. This means a tremendous gap between the somewhat hypothetical Primofilices, on the one hand, and the Cycadofilicales and Cordaitales, as we know them, on the other hand, a gap which there seems to be small probability of filling up with intermediate forms. In this presentation the only thing possible is to take the ovules of the investigated Paleozoic forms as representing the oldest known ovules, and to note the general changes that have occurred since.

To select the most primitive type of ovule from among the Paleozoic forms that have been investigated is impossible, unless it is assumed that those ovules which are most unlike the modern ones represent the most primitive type. This may or may not be true, but it is the only available criterion; and by using it, we obtain the following result. The oldest ovule had a single integument entirely free from the nucellus; in testa-formation this integument differentiated into three layers, the outer fleshy, the stony, and the inner fleshy; the ovule was supplied with two sets of vascular strands, the outer set traversing the outer fleshy layer, and the inner set traversing the peripheral region of the nucellus; and the beaked tip of the nucellus broke down more or less completely within the firm and resistant epidermis to form a pollen chamber. If these are really the features of the most primitive known ovules, the changes become very apparent, and they represent general tendencies, for they appear in every phylum.

In the first place, the integument and nucellus, instead of remaining separate, develop separately only in the region of the nucellar beak. So early was this change that it probably represents the condition of the majority of the Paleozoic ovules, a condition which has persisted ever since. The method of development is very evident, the integument appearing first as a distinct annular growth about the base of the young nucellus, but later its basal meristematic zone becoming indistinguishable from that of the nucellus. In all probability the change was brought about by the earlier appearance of the integument, and the result has been more or less variability in the amount of freedom from the nucellus.

The three-layered testa persists remarkably throughout gymnosperms, varying chiefly in the amount of development of the outer fleshy layer. The stony layer is always strongly developed, and at the maturity of the seed the inner fleshy layer always forms for it a papery lining. A strong development of the outer fleshy layer, resulting in fleshy seeds, continues throughout the cycadophyte phylum and the Ginkgoales and is a feature of many of the Taxaceae. Among the Pinaceae the outer fleshy layer is present in the young integument, but does not develop, so that the stony layer is the conspicuous superficial feature of the seed. The development of the outer fleshy layer among the Cycadales and Ginkgoales is phylogenetically continuous from the Cycadofilicales and Cordaitales; but among the Taxaceae there is probably no such continuity, but a reappearance of the activity of this layer in certain genera. Among the Gnetales, the single integument of the other gymnosperms is replaced by two integuments, the inner fleshy layer having become differentiated as a delicate inner integument, which appears earlier than the heavier outer integument, which gives rise to the outer fleshy and stony layers. In Gnetum the outer fleshy layer develops the pulpy investment characteristic of the primitive seeds; but in Ephedra this layer behaves as among the Pinaceae. If any general tendencies can be inferred from these facts in reference to the integument and testa they are seen in the abortion of the outer fleshy layer in the largest group of living gymnosperms, and in the final differentiation of the three-layered integument into two integuments.

The vascular supply of the ovule exhibits a very evident progressive change. When the integument and nucellus become free only in the region of the nucellar beak, the inner set of vascular strands is shifted from the peripheral region of the nucellus to the inner fleshy layer, and this situation persists among the cycadophytes. Curiously enough, it reappears in Gnetum, but in that case it is associated with the presence of the two integuments. Among Ginkgoales the outer set of strands is suppressed; among Taxaceae the inner set is suppressed; and among Pinaceae both sets have disappeared. The general tendency, therefore, is to eliminate the vascular strands from the ovule; but it is puzzling to find both sets absent from the older Abietineae, and one set still present among the younger Taxineae.

The presence of a pollen chamber is one of the most conspicuous features of the primitive ovule, and its association with fertilization by ciliated sperms is so evident that it is natural that the two disappeared simultaneously with the establishment of Coniferales, but the abruptness of the disappearance is evidently more apparent than real. The presence of an extraordinarily deep pollen chamber in Ephedra can hardly be regarded as a contradiction to this general statement, for in that case it is evidently of secondary origin, associated with a remarkably massive archegonium neck.

THE FEMALE GAMETOPHYTE

The female gametophyte of gymnosperms exhibits a progressive series of changes which is significant because it leads toward the angiosperm condition. At this point the very important historical record fails, and the entire testimony must be obtained from living forms, which do not represent a series, but the ends of many series. For this reason, and also because such progress is always very unequal in different forms, various stages of advancement may be expected to be found in forms grouped in a single alliance. The series, therefore, is not so much one which conforms to recognized groups, as a series of stages each of which may be exhibited by members of various groups.

The general development of the gametophyte is quite uniform; and since the same sequence of events occurs among the heterosporous pteridophytes, it may be inferred that a knowledge of the ancient gymnosperms would not materially change this situation. The general sequence referred to in the development of the gametophyte is as follows: free nuclear division, usually accompanied by vacuolation which results at some stage in parietal placing; the formation of walls, resulting in a parietal tissue; the centripetal growth of this tissue until it reaches the center of the embryo sac; and the final growth of the gametophyte until it reaches its mature size. In certain cases there may be no parietal placing, the free nuclei remaining distributed throughout the embryo sac; and therefore there is no centripetal growth, but general wall-formation throughout the sac. The details of the formation of permanent endosperm tissue from the primary walled cells are variable and perhaps very important from the evolutionary point of view, but the range of forms from which these details have been obtained is far too small to make them of present service in this connection.

The tendency which runs through gymnosperms as a whole, and which reaches its extreme expression among angiosperms, is to mature the eggs earlier and earlier in the ontogeny of the gametophyte. In the most primitive condition of the gametophyte, the eggs do not appear until the endosperm is nearly full grown; and other gametophytes can be selected and arranged in a series showing the gradual slipping-back of the egg in the ontogeny of the gametophyte, until in such a form as Torreya the archegonium initial is differentiated as soon as wall-formation has taken place. A conspicuous illustration of the inequality of response to such a general tendency among related forms is furnished by Torreya and Cephalotaxus, the archegonia not appearing in the latter genus until the gametophyte is well grown. The next stage is illustrated by the situation in Tumboa, in which eggs are matured before wall-formation is complete, resulting in the elimination of archegonia. The extreme stage in this progressive series of changes among gymnosperms is illustrated by Gnetum, in which eggs are matured at the stage of free nuclear division, the most embryonic stage of the female gametophyte.

So far as the living forms are concerned, the Cycadales and Ginkgoales show little, if any, response to this tendency; and therefore possess the most primitive type of female gametophyte among living gymnosperms. Among the Coniferales, on the other hand, all stages are found, to the one just preceding the elimination of archegonia; and this stage is attained by Tumboa and Gnetum.

The general tendency of the archegonia among gymnosperms is to eliminate the ventral canal cell. The gymnosperms are distinguished from the pteridophytes by the complete elimination of neck canal cells, and this tendency to suppress all of the axial row except the egg continues among gymnosperms. Among the living forms, a walled ventral canal cell is retained only among the Abietineae, so far as known; but it seems to be a safe inference that it was present among the ancient gymnosperms. In the other living groups the wall has disappeared, and the ventral canal cell is represented by a free nucleus. In certain forms even this nucleus may have disappeared; and of course there is no trace of it when the archegonia are eliminated.

The distribution of archegonia may be considered in this connection, although the tendencies do not appear general. It is becoming evident that the position of archegonia is related to the position of the pollen tube, which often reaches the embryo sac before the archegonium initials are selected. In cases where the pollen tube assumes a lateral position in reference to the gametophyte (as in Sequoia and Widdringtonia), it has been demonstrated that the latter responds by the selection of numerous deep-seated and laterally placed archegonium initials. It may be inferred, therefore, that the usual micropylar position of archegonia is due to the usual micropylar position of the tip of the pollen tube. It may be that numerous scattered and rather indefinitely placed archegonia were a feature of ancient gymnosperms, but there is no evidence for it; on the contrary, the few sections of Paleozoic ovules that reveal archegonia, and also the archegonia of heterosporous pteridophytes, suggest the opposite conclusion. In any event, they tend to become definite in number and are then organized in two ways: either as individual archegonia, each with its own jacket and chamber; or as an archegonial complex, with a common jacket and chamber. The latter may seem to be a specialized condition, exhibited chiefly by Cupressineae, but it also seems to be the natural condition from which to derive the free eggs of Tumboa and Gnetum when archegonia are eliminated from ontogeny.

THE MALE GAMETOPHYTE

It is perhaps impossible as yet to determine the character of the male gametophyte of the Paleozoic gymnosperms. The evidence is accumulating that it comprised many more cells than do the gametophytes of most living gymnosperms; but it is not demonstrable whether these supernumerary cells were vegetative or spermatogenous. There are instances of supernumerary cells of both kinds among living gymnosperms, so that they furnish no clue; and the same is true of heterosporous pteridophytes. The balance of probability, however, is in favor of the view that they were in the main spermatogenous.

In any event, starting with the known condition among heterosporous pteridophytes, the tendency among gymnosperms has been to reduce and finally to eliminate the vegetative (prothallial) tissue; and to reduce the sperm mother cells to two.

In certain groups (as Abietineae) the prothallial cells are two in number; in others (as cycads) there is one prothallial cell; and in still others (as Taxodineae, Cupressineae, and Taxineae) prothallial tissue has been eliminated. Such prothallial cells as do appear are sometimes persistent and sometimes ephemeral; so that the evidence of a disappearing tissue is complete, and it actually has disappeared in what are recognized as the most modern groups. The situation common to Podocarpineae and Araucarineae is usually cited as an illustration of a more extensive and therefore a more ancient prothallial tissue, which connects directly with the "multicellular" pollen grains of Cordaitales. This may be true, but all of the extra cells are derived from two primary ones, which hold a definite place in the ontogeny of the gametophyte; and therefore may represent a secondary tissue that holds no phylogenetic relation to the more extensive prothallial tissues of older forms. In any event, it is ephemeral, breaking down and liberating its nuclei.

The number of sperm mother cells is so rigidly two, that this reduction may be said to have been accomplished by all living gymnosperms, whatever may be the fact in reference to the Paleozoic gymnosperms. It is interesting to note that the very few instances of a greater number of sperm mother cells occur in one group characterized by its retention of ancient features (Cycadales), and in another group characterized by its very modern features (Cupressineae). While phylogenetic continuity of multiple sperms might be claimed for Cycadales, no such claim could be maintained for Cupressineae.

The greatest epoch in the history of the male gametophyte of gymnosperms, however, was the abandonment of ciliated sperms, and this occurred in connection with the establishment of Coniferales. It is not generally appreciated that five of the seven recognized primary groups of gymnosperms possess ciliated sperms, and that the modern type or completely terrestrial type of sperm was introduced by the conifers. This also affected the pollen chamber, the pollen tube, and the cell generations in spermatogenesis. The pollen chamber disappeared; the pollen tube ceased to be exclusively a branching haustorial organ and became a sperm-carrier; while the last cell-generation in spermatogenesis was omitted. It is this condition of spermatogenesis that is carried forward by angiosperms to a still greater stage of reduction. Just what cells are eliminated and what cells remain is a question of small importance. The significant fact is that spermatogenesis is shortened, and the ultimate cells, although non-ciliated, are physiologically sperms.

THE EMBRYO

The absence of embryos from the seeds of Paleozoic gymnosperms indicates that some great change connected with embryo-formation was introduced by the Mesozoic gymnosperms. It would be of extreme interest to know the ancient condition, but we know only what it has become. After this change, whatever it may have been, the proembryo has become the structure showing steady and progressive change.

The first stage in the development of the proembryo is free nuclear division, followed by wall-formation; and in the most primitive condition the free nuclei are so numerous that wall-formation results in a tissue which fills the egg. The tendency is to reduce the number of free nuclear divisions, resulting in a reduction of the amount of proembryonic tissue, so that more and more of the general cytoplasm of the egg is left free from tissue. The proembryo of Ginkgo has retained a very primitive character; and illustrations of early stages in the reduction of the proembryo may be observed among the cycads.

In Zamia, for example, which illustrates the extreme amount of reduction among cycads, the proembryo is a relatively small amount of tissue at the base of the egg. Among the Coniferales this reduction has been carried forward to a much greater extent, 16 free nuclei appearing sometimes, 8 free nuclei being the prevailing number, and 4 free nuclei being occasionally attained. This results in a proembryo consisting of a small and definite number of cells, with distinctly distributed functions. Now and then among gymnosperms (as in Sequoia), there is no free nuclear division, but these are interesting rather than significant exceptions. Even among the Gnetales it is found that a certain amount of free nuclear division precedes wall-formation. That this reduction of the free nuclei before wall-formation is significant, is shown by the fact that among angiosperms free nuclei have disappeared, and wall-formation accompanies the first division of the egg-nucleus.

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